Final Report for Period: 02/2009 - 08/2009 **Submitted on:** 12/01/2009

Principal Investigator: Jiang, Lin . **Award ID:** 0640416

Organization: GA Tech Res Corp - GIT

Submitted By:

Jiang, Lin - Principal Investigator

Title:

Competition for Biotic Resources and Coexistence in Variable Environments

Project Participants

Senior Personnel

Name: Jiang, Lin

Worked for more than 160 Hours: Yes

Contribution to Project:

As the PI, Jiang coordinated the project and trained postdocs, graduate and undergraduate students during the course of the project. In addition, he has also done conceptual, theoretical, meta-analytical, and experimental work partially supported by the project.

Post-doc

Name: Violle, Cyrille

Worked for more than 160 Hours: No

Contribution to Project:

Violle conducted an experiment examining the importance of competition along disturbance gradients and a bioinformatical analysis of bacterial functional trait evolution.

Name: Ryberg, Wade

Worked for more than 160 Hours: No

Contribution to Project:

Ryberg completed two protist microcosm experiments, one on community assembly involving predators and prey, and the other on species tradeoffs at local and regional scales.

Graduate Student

Name: Pu, Zhichao

Worked for more than 160 Hours: Yes

Contribution to Project:

Pu has been supported by this project as a graduate student. He has been primarily responsible for designing the chemostats and running the proposed long-term competition experiments. He also completed a theoretical analysis of phytoplankton-zooplankton coevolution along productivity gradients.

Name: Tan, Jiaqi

Worked for more than 160 Hours: No

Contribution to Project:

Tan completed two microbial microcosm experiments, one on the functional significance of species diversity at two trophic levels (bacteria and bacterivorous protists) and the other on testing Darwin's naturalization hypothesis in bacterial communities.

Undergraduate Student

Name: Rajendra, Chathruckan

Worked for more than 160 Hours: No

Contribution to Project:

Rajendra (fall 2007) investigated whether the presence of bacterivorous consumers would alter the relationship between microcosm size and diversity of culturable bacteria.

Name: Flakes, Sooyung

Worked for more than 160 Hours: No

Contribution to Project:

Flakes investigated how the history of community assembly affects community dynamics (spring 2008, together with Joshi) and how assembly history affects the structure of meta-communities (fall 2008).

Name: Jung, yeonjin

Worked for more than 160 Hours: No

Contribution to Project:

Yeonjin Jung (spring 2009, collaborating with Stallings) conducted an experiment to examine how disturbance affects the role of history of community assembly in modulating community structure.

Name: Stallings, Carrie

Worked for more than 160 Hours: No

Contribution to Project:

Carrie stallings (spring 2009, collaborating with Jung) conducted an experiment to examine how disturbance affects the role of history of community assembly in modulating community structure.

Name: Patel, Harsh

Worked for more than 160 Hours: No

Contribution to Project:

Patel (spring, summer 2009) examined the assembly of protist communities containing both bacterivorous and predatory protists in the absence and presence of dispersal among local communities.

Name: Lee, Janet

Worked for more than 160 Hours: No

Contribution to Project:

Lee conducted two experiments: one on the assembly of bacterivorous protist communities (spring 2009), and the other on the competition of two predatory protist species on a single prey protist species with and without dispersal among communities (summer 2009).

Technician, Programmer

Other Participant

Research Experience for Undergraduates

Name: Patel, Shivani

Worked for more than 160 Hours: Yes

Contribution to Project:

Patel (REU student, summer 2007) used protist microcosms to examine the combined effects of disturbance and predation on species diversity. In collaboration with Joshi, she also investigated how predation affects the relationship between biodiversity and temporal stability (spring 2007).

Years of schooling completed: Junior

Home Institution: Same as Research Site

Home Institution if Other:

Home Institution Highest Degree Granted(in fields supported by NSF): Doctoral Degree

Fiscal year(s) REU Participant supported: 2007

REU Funding: REU supplement

Name: Joshi, Hena

Worked for more than 160 Hours: Yes

Contribution to Project:

Patel (REU student, summer 2007) used protist microcosms to examine the combined effects of disturbance and predation on

species diversity. In collaboration with Joshi, she also investigated how predation affects the relationship between biodiversity and temporal stability (spring 2007).

Years of schooling completed: Freshman

Home Institution: Same as Research Site

Home Institution if Other:

Home Institution Highest Degree Granted(in fields supported by NSF): Doctoral Degree

Fiscal year(s) REU Participant supported: 2008

REU Funding: REU supplement

Name: Brady, Lauren

Worked for more than 160 Hours: Yes

Contribution to Project:

Brady (REU student supported by a chemical ecology REU program at Georgia tech [PI-Julia Kubanek], summer 2009) investigated the combined effects of species diversity and assembly history in resident communities on the success of invading species.

Years of schooling completed: Sophomore

Home Institution: Other than Research Site

Home Institution if Other: Kenyon College

Home Institution Highest Degree Granted(in fields supported by NSF): Bachelor's Degree

Fiscal year(s) REU Participant supported: 2009

REU Funding: REU site award

Organizational Partners

Other Collaborators or Contacts

Activities and Findings

Research and Education Activities:

The main goal of this project was to provide experimental evaluations of the non-equilibrium theory of species coexistence, using communities of bacteria and bacterivorous protists as model systems. In particular, we proposed to specifically test whether relative nonlinearity, namely differential, nonlinear species responses to changes in resource availability, constitutes a legitimate mechanism contributing to species coexistence. Towards this goal, we have measured numerical responses of more than a dozen bacterivorous protist species on a single bacterium Serratia marcescens, identified several pairs of bacterivorous protist species exhibiting the gleaner-opportunist trade-off on Serratia (i.e., one species grows faster at low Serratia densities and the other species grows faster at high Serratia densities; a necessary condition, as predicted by theory, for the relative nonlinearity to promote species coexistence), and established chemostat systems for running long-term experiments that are necessary for evaluating species coexistence. We initially planned to use semi-continuous cultures, but switched to continuous chemostat cultural techniques because frequent samplings from our semi-continuous cultures introduce unwanted bacterial contaminants. We have resolved technical problems associated with chemostat maintenance that prevented us from running our proposed long-term experiments in the past. Using the chemostats, we have collected data on long-term (more than 80 days, collected daily) population dynamics of a gleaner-opportunist pair (Colpidium striatium and Tetrahymena pyriformis, grown on Serratia marcescens) in competition as well as in isolation under a single dilution rate. Although the project has ended, we plan to continue running the long-term experiment with the same species pair at different dilution rates and with other gleaner-opportunist pairs at multiple dilution rates. We also plan to run the experiment with more than two bacterivorous protist species competing for a single bacterial species, which would allow the evaluation of the importance of relative nonlinearity in promoting species coexistence in more diverse communities, and with bacterivorous protists competing for multiple bacterial species, which would allow the evaluation of the relative importance of relative nonlinearity and niche differentiation in maintaining species diversity. By doing so, we hope to attain a thorough understanding of the role of relative nonlinearity in modulating species coexistence and diversity.

This grant also provided partial support for other research activities conducted by the PI (Lin Jiang), two postdocs (Cyrille Violle and Wade

Ryberg), two graduate students (Zhichao Pu and Jiaqi Tan), and nine undergraduate students (Shivani Patel, Hena Joshi, Sooyung Flakes, Chathruckan Rajendra, Yeonjin Jung, Carrie Stallings, Harsh Patel, Janet Lee, and Lauren Brady), resulting in 9 publications, 3 manuscripts currently under review, 3 manuscripts in draft, and several other completed experiments that may produce additional publications. The topics of each person involved in this project are listed below.

PI's research

This grant supported the PI's conceptual work on the relationship between biodiversity and ecosystem functioning, theoretical work on the stimulatory effect of protist grazing on bacteria-mediated organic matter decomposition, meta-analysis of the relationship between biodiversity and temporal stability, and experimental work on the role of phylogenetic relatedness between resident and invading species in determining community invasibility, and bacterial community assembly.

1) Conceptual development:

a. A large part of research on biodiversity and ecosystem functioning has focused on the effect of species diversity on biomass production, giving the impression that there tends to be a generally positive diversity-function relationship. Based on my experimental work on bacterial diversity and function (Jiang 2007, Ecology) and related work from the literature, I have developed a conceptual model in which ecosystem functioning can exhibit various relationships with species diversity. I have suggested that this lack of a general relationship between biodiversity and ecosystem functioning may arise from the operation of the negative selection effect overwhelming or counteracting effects of niche complementarity (Jiang et al. 2008, Oikos).

b. While productivity tends to increase with species diversity in experiments that directly manipulated diversity, various patterns of productivity-diversity relationships have been observed in natural communities. This discrepancy cannot be fully explained by the existing hypotheses that have been put forward to account for it. In a recent conceptual paper (Jiang et al. 2009, Journal of Ecology), I formulated three novel hypotheses, focusing on the importance of selection effects, complementarity, and competitive exclusion, to explain this difference between results of diversity-manipulation experiments and natural patterns.

2) Theoretical model:

Protist grazing on bacteria has long been known to promote bacteria-mediated decomposition of organic matter, but mechanisms underlying this pattern have been largely conjectural. One popular hypothesis is that grazing recycles limiting nutrients that benefit bacterial growth. To examine this hypothesis, I collaborated with a mathematician (Hao Wang) and a theoretical ecologist (Joshua Weitz) at Georgia tech to develop a theoretical model that incorporates different stoichiometries between bacteria and their grazers (Wang et al. 2009, FEMS Microbiology Ecology). We also compared our model predictions to results of existing empirical studies on the effects of protist grazing on decomposition.

3) Meta-analytic work:

The relationship between biodiversity and stability is a long-standing question in ecology. Historically, attempts to answer this question have been hampered by the presence of multiple, potentially confounding, stability concepts, confusion over responses at different levels of ecological organization, discrepancy between theoretical predictions, and particularly the paucity of empirical studies. In collaboration with my graduate student Zhichao Pu, I used meta-analyses to synthesize results of 29 empirical studies, published primarily in the past two decades, on the relationship between species diversity and temporal stability at both population and community levels (Jiang and Pu 2009, American Naturalist). We asked the question whether the relationship differs between terrestrial and aquatic studies, between observational and experimental studies, and between single- and multi-trophic studies.

4) Experimental work:

a. In The Origin of Species, Darwin (1859) proposed that non-native species should be less successful in invading native communities where their close relatives are present. This original hypothesis (often termed Darwin's naturalization hypothesis), which was based on another hypothesis of Darwin that competition tends to be stronger between more closely related species, has never been experimentally tested. Observations of natural communities have provided mixed support for this hypothesis. Using laboratory bacterial communities as model systems, we conducted the first experimental test of the hypothesis by manipulating phylogenetic relatedness of invading and resident species and examining the success (measured by both establishment and abundance) of the invading species in relation to its phylogenetic relatedness to resident communities (Jiang et al., American Naturalist, in press).

b. Previous studies of community assembly have focused on community structure and largely ignored ecosystem functions, despite that ecosystem function and community structure may be tightly linked (i.e., ecosystem functions may likely differ among communities characterized by different species composition and abundance). In light of this, I conducted a laboratory microcosm experiment to examine the role of the history of bacterial community assembly on bacterial community structure and bacteria-mediated organic matter decomposition. This experiment manipulated the order of introduction of four bacterial species and the presence/absence of a bacterivorous protist consumer Tetrahymena pyriformis, to test the hypotheses that bacterial communities with different assembly histories may differ in both structure (species composition and abundance) and function (decomposition) and that the presence of bacterivorous consumers may alter the importance of priority effects.

Cyrille Violle's research

This grant supported the research of Cyrille Violle, who was in the PI's lab as a postdoc between March 2008 and Dec 2008. During this time, Violle completed two projects, one experimental and the other bioinformatical.

1) Experimental work:

A common perception among ecologists is that competition is not important in structuring ecological communities in habitats strongly influenced by disturbance. Limited theory, however, suggests that the importance of competition may not necessarily decline with disturbance. In collaboration with Pu and the PI, Violle conducted the first experimental test of the importance of competition along a broad disturbance gradient in protist microcosms. To this end, we performed a series of experiments to measure body size, intrinsic growth rate, carrying capacity, competitive ability (as determined by outcomes of pair-wise competition experiments), and the ability to resist mortality-causing disturbances for 11 common bacterivorous ciliated protists, and monitor the densities of these species in competition along a gradient of disturbance (imposed by sonications differing in intensity). This work is currently under review in Nature (Violle, Pu and Jiang, Nature, in review). The results of these experiments also allowed us to test Darwin's hypothesis that competitive exclusion becomes more frequent between competing species that are more closely related (Violle, Pu and Jiang, PNAS, in review).
2) Bioinformatical work:
Violle applied the trait-based approach, which he used in his Ph.D. research on plants, to bacteria by linking bacterial phylogeny with metabolic traits. This was done by taking advantage of the Biolog database that contains information on the utilization pattern of hundreds of bacterial species on 95 carbon substrates. Violle mapped these bacterial functional traits onto bacterial phylogeny constructed based on sequence analysis of bacterial 16s rRNA genes. This work aimed to examine the following hypotheses: (i) bacterial communities are generally less phylogenetically clustered than plants and animals due to the commonness of horizontal gene transfer, but horizontal gene transfer does not prevent phylogenetic clusterness, especially for bacterial assemblages that exhibit relatively uncommon traits (i.e., the ability to utilize rare carbon compounds), and (ii) common ancestors of bacteria were metabolically complex, and evolve by losing functional traits gradually.

Wade Ryberg's research
Ryberg joined the PI's lab as a postdoc in June 2009, and has since completed two protist microcosm experiments, one on community assembly involving both predators and prey, and the other on species tradeoffs at local and regional scales.
1) A large amount of work has been done on the ecological effects of the history of community assembly, demonstrating its importance for structuring ecological communities. Few empirical assembly studies, however, have involved both predators and prey. The few experiments that did consider predator-prey interactions have focused on the assembly of prey communities, treating predators as static identities whose abundances do not change over the course of community assembly. Recognizing that predator abundances can change over time and that the history of predator colonization may also matter for community assembly, Ryberg conducted a protist microcosm experiment that manipulated the history of introduction of 10 bacterivorous protist species as well as the history of introduction of 3 predator protist species. He monitored the abundance of each predator and prey species weekly until communities reached steady state conditions.
2) Species often exhibit tradeoffs, including the competition-colonization tradeoff and the competition-disturbance tolerance tradeoff. The competition-colonization tradeoff has been considered as a regional tradeoff as it contributes to species coexistence at the regional scale, whereas the competition-tolerance tradeoff has been considered as a local tradeoff as it contributes to species coexistence at the local scale. It remains an open question whether the two tradeoffs would operate independently. Ryberg examined the possibility of the inter-dependence of the two tradeoffs in bacterivorous protists, which are known to exhibit both types of the tradeoffs. He measured species competitive ability by examining competitive outcomes in species pairwise interactions, quantified species dispersal abilities by measuring their rates of dispersal in inter-connected microcosms, and estimated species tolerance to disturbance by monitoring species density responses to sonication.

Zhichao Pu's research:
This grant supported the research of Zhichao Pu, a fourth-year graduate student in the PI's lab, on the theoretical analysis of phytoplankton-zooplankton coevolution. Based on the PI's previous theoretical work on adaptive evolution of plankton (Jiang et al. 2005, American Naturalist), Pu used both analytic tools and computer simulation to examine patterns of adaptive radiation of phytoplankton and zooplankton along a productivity gradient. He has manipulated environmental productivity, the presence and absence of zooplankton, and mutation rate to examine conditions under which different productivity-diversity patterns may emerge in both deterministic and stochastic models.

Jiaqi Tan's Research:
Jiaqi Tan joined the PI's lab in fall 2008 as a graduate student, and has since completed two microbial microcosm experiments partially supported by this grant. In one experiment, he manipulated species diversity of bacteria (4 species total) and bacterivorous protist species (3 species total) to examine their effects on bacterial community structure and organic matter decomposition. In another experiment, he manipulated species diversity and composition of bacterial communities and subjected these communities to invasion of an alien bacterial species to test Darwin's naturalization hypothesis.

Below are the brief summaries of research conducted by undergraduate students, who worked largely as independent researchers in the PI's lab to earn research credits. They all conducted protist microcosm experiments.

This grant supported the research by Shivani Patel and Hena Joshi in the spring of 2007. Using protist communities with different trophic levels assembled in laboratory microcosms, Patel and Joshi investigated how predation affects the relationship between biodiversity and temporal stability.

Shivani Patel (REU student, summer 2007) conducted an independent project to examine the combined effects of disturbance and predation on species diversity. This project addressed two questions: whether predation would alter the relationship between disturbance and diversity and whether the effects would differ between generalist and specialist predators.

This grant supported the research by Chathruckan Rajendra in the fall of 2007. By establishing laboratory microcosms with water samples from local ponds, Rajendra investigated whether the presence of bacterivorous consumers would alter the relationship between microcosm size and diversity of culturable bacteria.

This grant supported the research done by Hena Joshi and Sooyung Flakes in spring 2008. Previous work on community assembly has indicated that differences in the history of community assembly can lead to alternative stable states, in which equilibrial communities differ in species composition and/or abundances. An interesting, but previously unexplored hypothesis is that not only alternative stable states, but also alternative dynamic states (i.e., different population dynamics) can emerge in communities subject to different assembly histories. To test this idea, Joshi and Flakes conducted a laboratory microcosm experiment with one predator protist species and three bacterivorous protist species as the prey, in which prey species colonization history and environmental productivity were manipulated.

This grant supported Hena Joshi as an REU student in the summer of 2008. Building on her research in spring 2008 and recognizing that community assembly studies have not examined the role of predator colonization history, Hena independently conducted a protist microcosm experiment that manipulated both predator and prey colonization histories.

This grant supported the research by Sooyung Flakes in fall 2008, who expanded her spring 2008 work to examine the assembly of meta-communities. Natural communities are open to species dispersal at both meta-community and local community scales, but how these two aspects of species dispersal combine to influence local community structure and population dynamics remains empirically unexplored. Flakes investigated this question with the same protist species that she used in spring 2008, by manipulating both the order of species introduction and the magnitude of species dispersal between local communities.

Harsh Patel (spring, summer 2009) examined the assembly of protist communities containing both bacterivorous and predatory protists in the absence and presence of dispersal among local communities.

Janet Lee (spring, summer 2009) conducted two experiments: one on the assembly of bacterivorous protist communities (spring 2009), and the other on the competition of two predatory protist species (Dileptus anser and Lacymaria olor) on a single prey protist species (Tetrahymena pyriformis) with and without dispersal among communities.

Yeonjin Jung and Carrie stallings (spring 2009) conducted an experiment to examine how disturbance (in the form of sonication) affects the role of history of community assembly in modulating community structure. This experiment differed from another experiment on the same subject (Jiang and Patel 2008, Ecology) by varying the intensity of disturbance, not the microcosm volume subjected to disturbance of the same intensity as in Jiang and Patel (2008).

Lauren Brady (REU student supported by a chemical ecology REU program at Georgia tech [PI-Julia Kubanek], summer 2009) investigated the combined effects of species diversity and assembly history in resident communities on the success of invading species.

Findings:

The PI's research:
1) Conceptual development:
a. In Jiang et al. (2008, Oikos), I proposed that ecosystem functioning may not necessarily increase with biodiversity, challenging the positive relationship between biodiversity and productivity as documented by many theoretical and experimental studies. Specifically, I suggested that the diversity-function relationship may be positive, negative, or neutral, depending upon the strength of the negative selection effect and that negative and neutral relationships would be relatively common for functions not tightly linked with species biomass. The latter prediction was based on the rationale that strong negative selection effects may frequently operate in situations where strong competitors, which often attain large biomass, contribute relatively little to the non-biomass functions of interest.
b. In Jiang et al. (2009, Journal of Ecology), I proposed that different diversity-productivity relationships between diversity-manipulation experiments and natural observations can be explained by the difference in the importance of niche complementarity, selection effects, and competitive exclusion. I suggested that results from diversity-manipulation experiments may not necessarily apply to natural communities because (1) niche complementarity is less important in natural communities because of unequal abundances among species, (2) the positive selection effect is less important in natural communities because of the wide distribution of abundant species, and (3) competition is more likely to run its full course in natural communities, resulting in more frequent competitive exclusion.

2) Theoretical model:
In Wang et al. (2009, FEMS Microbiology Ecology), we developed a bacteria-grazer model of organic matter decomposition that incorporates protozoa-driven nutrient recycling and stoichiometry. Our model shows two principal results: (1) when the environment is carbon limiting, organic matter can always be decomposed completely, regardless of the presence/absence of grazers; (2) when the environment is nutrient (such as nitrogen) limiting, it is possible for organic matter to be completely decomposed in the presence, but not absence, of grazers. Grazers facilitate decomposition by releasing nutrients back into the environment, which would otherwise be limiting, while preying upon bacteria. Our model analysis also reveals that facilitation of organic matter decomposition by grazers is positively related to the stoichiometric difference between bacteria and grazers.
3) Meta-analytic work:
In Jiang and Pu (2009, American Naturalist), we showed that, through the meta-analysis of 29 empirical studies, that the overall effect of increasing species diversity was positive for community-level temporal stability but neutral for population-level temporal stability. There were, however, striking differences in the diversity-stability relationship between single- and multitrophic systems, with diversity stabilizing both population and community dynamics in multitrophic, but not singletrophic communities. These patterns were broadly equivalent across experimental and observational studies as well as across terrestrial and aquatic studies.
4) Experimental work:
a. In Jiang et al. (American Naturalist, in press), we reported on the first experimental test of Darwin's naturalization hypothesis in laboratory bacterial communities varying in phylogenetic relatedness between resident and invading species with and without a protist bacterivore. Consistent with this hypothesis, invasion success increased with phylogenetic distance between the invading and resident bacterial species, both in the presence and absence of protistan bacterivory. The frequency of successful invader establishment was best explained by average phylogenetic distance between the invader and all resident species, indicating limitation by the availability of unexploited niche; invader abundance was best explained by phylogenetic distance between the invader and its nearest resident relative, indicating limitation by the availability of unexploited optimal niche. These results were largely driven by one resident bacterium (a subspecies of Serratia marcescens) posting the strongest resistance to the alien bacterium (another subspecies of S. marcescens). Overall, our findings support phylogenetic relatedness as a useful predictor of species invasion success.
b. Results from the bacterial assembly experiment conducted by the PI showed that communities with different assembly histories differed in bacterial species abundances, but not in species composition. However, this history-induced difference in bacterial species abundances did not translate into differences in organic matter decomposition. The presence of bacterivorous consumers increased the degree of organic matter decomposition, but did not alter the effect of history on bacterial community structure or decomposition. The abundance of bacterivorous consumers, which did not differ among communities with different histories, showed a strong positive correlation with the degree of organic matter decomposition. Both consumer abundance and organic matter decomposition demonstrated substantial variation within assembly history treatments, suggesting random divergence among communities experiencing the same histories.

Cyrille Violle's research:
1) Experimental work:
A series of experiments on interspecific competition between bacterivorous protist species have yielded some novel and exciting results. In Violle et al. (Nature, in review), we report that disturbance does not diminish the importance of competition. More specifically, interspecific competition significantly increased rates of species extinction over a broad disturbance gradient, and increasing disturbance intensities increased, rather than decreased, the tempo of competitive exclusion. This community-level pattern is linked to the species-level pattern that interspecific competition led to most frequent extinctions of each species at the highest level of disturbance that the species can tolerate. As a result, despite a strong trade-off between competitive ability and disturbance tolerance across the competing species, species diversity declined with disturbance. In Violle et al. (PNAS, in review), we report that both the probability and rate of competitive exclusion significantly increased with phylogenetic relatedness of the competing species. This result was explained by the tendency of closely related species to share similar body size, a trait strongly related to species competitive ability. Our results support Darwin's hypothesis that phylogenetic similarity is a useful predictor of the outcomes of competitive interactions in ecological communities.
2) Bioinformatical work:
The analysis of the carbon substrate utilization patterns of bacterial species revealed that bacteria deeper in the phylogeny were able to use a greater variety of carbon compounds, suggesting that common ancestors of bacteria may be metabolically complex. This result was robust to the random placement of a number of lineages in the phylogenetic tree.

Wade Ryberg's research:
1) Ryberg's trophic assembly experiment showed that both the history of predator introduction and the history of prey introduction affected species abundances, leading to rather complex, sometimes idiosyncratic, community patterns. In several cases, predator history effects overwhelmed the prey history effect.
2) Ryberg's experiment on tradeoffs in bacterivorous protists revealed that the competition-colonization tradeoff and the competition-disturbance tolerance tradeoff were not independent. In particular, increasing levels of disturbance reduced the strength of competition-colonization tradeoff. At the species level, disturbance affected the competitive rank and colonization rank of species differently.

Zhichao Pu's research:
Pu's theoretical work on plankton evolution showed that evolutionary branching of phytoplankton can only occur in the presence, but not absence, of zooplankton. Evolutionary branching of phytoplankton populations was followed by evolutionary branching of zooplankton populations. In both deterministic and stochastic models, this coevolution between phytoplankton and zooplankton resulted in increases of their species diversity with increasing productivity.

Jiaqi Tan's research:
In his experiment manipulating both bacterial diversity and bacterivorous protist species diversity, Tan found that specialist bacterivores, which can only survive with certain bacteria as the prey, were outcompeted by the generalist bacterivore that can feed on a variety of bacterial prey. The transient presence of specialist bacterivores, however, altered the structure of bacterial communities, making it different from that of bacterial communities with only the generalist bacterivore. Protist bacterivory increased decomposition such that there was a positive relationship between bacterivore biovolume and wheat seed decomposition.
In his experiment testing Darwin's naturalization hypothesis in bacterial communities, Tan found that phylogenetic relatedness of the invading species and resident communities played a relatively small role, compared with resident species abundance and diversity, in determining invasion success. This result challenges the generality of Darwin's naturalization hypothesis, supported by our previous experiment (Jiang et al., American naturalist, in press).

Undergraduate research:
Patel and Joshi (spring 2007) examined the effect of predation on the relationship between biodiversity and stability. Their experimental data revealed that predation significantly altered the relationship between biodiversity and temporal variability at both the population and community level. Predation changed a negative diversity-stability relationship at the population level to a neutral one, and changed a neutral diversity-stability at the community level to a positive one. This work has been published in the American Naturalist with Joshi and Patel as coauthors (Jiang, Joshi and Patel 2009)

Patel's REU work (summer 2007) showed that predation did not alter the relationship between disturbance and diversity, and that generalist, but not specialist, predators reduced species diversity at all levels of disturbance. Interestingly, results in none of the predation treatments (no predator, generalist predator, and specialist predator) supported the intermediate disturbance hypothesis.

Data from Rajendra's experiment (fall 2007) revealed that predation affected the species-area relationship, which changed over the course of succession of bacterial communities. However, both the effects of predation and time were not consistent or predictable, possibly indicating the lack of refined techniques of the undergraduate in working with bacteria.

Hena Joshi and Sooyung Flakes (spring 2008) examined the effects of assembly history on community structure and population dynamics. Their results indicated that protist communities with different assembly histories differed in species composition and population dynamics. In communities in which a protist species that was competitively superior and most resistant to predation was introduced first, the predator species went extinct and the three prey species coexisted with steady population densities. In communities where a protist species that was competitively inferior and most edible to predators was introduced first, the other two prey species went extinct and the predator and the existing prey species exhibited population oscillations indicative of predator-prey cycles. This study is the first reporting that different dynamic states can arise from different community assembly histories (Jiang, Joshi, and Flakes, Ecology, in review). Joshi's REU experiment (summer 2008), which manipulated both predator and prey colonization histories, produced similar results.

The experiment of Sooyung Flakes (fall 2008), which manipulated both the history of community assembly and inter-community dispersal, found that increasing dispersal among local communities increased local species diversity and reduced beta-diversity of the meta-community. Also the oscillatory predator-prey dynamics were more long-lasting with higher levels of dispersal. Somewhat similar, but weaker results were found in similar experiments by Harsh Patel (spring, summer 2009).

Janet Lee (spring 2009) found that strong priority effect affected the assembly of bacterivorous protist communities, though communities eventually converged on similar species composition and abundance. The summer 2009 experiment of Lee demonstrated that the R* rule of resource competition also applies to situations where consumer-resource interactions lead to oscillatory population dynamics. The predatory protist species that reduced the prey abundance to the lower level always won in competition with another predatory protist species

The experiment of Yeonjin Jung and Carrie Stallings (spring 2009) was plagued by contamination and did not work out.

The experiment of Lauren Brady (REU student, summer 2009) found that increasing resident species diversity reduced community invasibility, but that priority effects associated with different community assembly histories played a more important role, with resident communities having the same species composition but different histories often having significantly different invader abundances. This experiment also supported the theoretical prediction that priority effects tend to be more common in more diverse communities.

Training and Development:

This project has involved two postdocs (Cyrille Violle and Wade Ryberg), two Ph.D. students (Zhichao Pu and Jiaqi Tan) and nine undergraduate students (Shivani Patel, Hena Joshi, Sooyung Flakes, Chathruckan Rajendra, Yeonjin Jung, Harsh Patel, Janet Lee, Lauren Brady, and Carrie Stallings). They received training on hypothesis testing, experimental design, data analysis, and manuscript writing.

Outreach Activities:

The PI's laboratory has accommodated visits from local middle school teachers. The PI demonstrated to these teachers that protist species and microcosms may be useful tools for conducting ecological experiments in their classrooms.

Journal Publications

Jiang, L. and S. N. Patel, "Community assembly in the presence of disturbance: a microcosm experiment", Ecology, p. , vol. 89, (2008). Published,

Jiang, L., Z. Pu, and D. R. Nemergut, "On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning", Oikos, p. , vol. 117, (2008). Published,

Jiang, L., H. Joshi and S. N. Patel, "Predation alters relationships between biodiversity and temporal stability. American Naturalist", American Naturalist, p. 389, vol. 173, (2009). Published,

Jiang, L; Wan, SQ; Li, LH, "Species diversity and productivity: why do results of diversity-manipulation experiments differ from natural patterns?", JOURNAL OF ECOLOGY, p. 603, vol. 97, (2009). Published, 10.1111/j.1365-2745.2009.01503.

Violle, C; Jiang, L, "Towards a trait-based quantification of species niche", JOURNAL OF PLANT ECOLOGY-UK, p. 87, vol. 2, (2009). Published, 10.1093/jpe/rtp00

Wang, H; Jiang, L; Weitz, JS, "Bacterivorous grazers facilitate organic matter decomposition: a stoichiometric modeling approach", FEMS MICROBIOLOGY ECOLOGY, p. 170, vol. 69, (2009). Published, 10.1111/j.1574-6941.2009.00699.

Jiang, L; Pu, ZC, "Different Effects of Species Diversity on Temporal Stability in Single-Trophic and Multitrophic Communities", AMERICAN NATURALIST, p. 651, vol. 174, (2009). Published, 10.1086/60596

Lin Jiang, Jiaqi Tan and Zhichao Pu, "An experimental test of Darwin's naturalization hypothesis", American Naturalist, p. , vol. , (2010). Accepted,

Cyrille Violle, Zhichao Pu and Lin Jiang, "Experimental demonstration of the importance of competition under disturbance", Nature, p. , vol. , (2010). Submitted,

Cyrille Violle, Zhichao Pu and Lin Jiang, "Phylogenetic limiting similarity and competitive exclusion", PNAS, p. , vol. , (2010). Submitted,

Lin Jiang, Hena Joshi, and Sooyung K. Flakes, "Alternative community compositional and dynamical states: the dual consequences of assembly history", Ecology, p. , vol. , (2010). Submitted,

Books or Other One-time Publications

Jiang., L., "Biodiversity and ecosystem functioning: beyond complementarity and positive selection effects.", (2009). Book, Published
Editor(s): Wu, J. and J. Yang
Collection: Lectures in Modern Ecology (IV): Theory and Applications
Higher Education Press, Beijing
Bibliography: Pages 38-57

Web/Internet Site

Other Specific Products

Contributions

Contributions within Discipline:

Understanding mechanisms maintaining species diversity is a major focus of community ecology. This project aims to use laboratory microcosm experiment to evaluate important coexistence mechanisms that remain largely untested. Our experimental results indicate that the gleaner-opportunist tradeoff exists among species, that consumer-resource interactions can lead to population fluctuations, and that long-term non-equilibrium coexistence was possible between one gleaner-opportunist pair at a single dilution rate. These results demonstrate that species displaying the gleaner-opportunist tradeoff can coexist on a single limiting resource, as predicted by theory, confirming the role of the relative nonlinearity as an important coexistence mechanism. Related research conducted by the PI, postdocs, graduate and undergraduate students, contribute to further understanding of the causes and consequences of biodiversity, the role of phylogenetic relatedness in influencing species interactions and community structure, the importance of competition along disturbance gradients, and the role of assembly history in the formation of alternative stable states and alternative dynamic states.

Contributions to Other Disciplines:

Contributions to Human Resource Development:

All but two undergraduates involved in this project were women. Thus we are contributing to the training of an under-represented group in science.

Contributions to Resources for Research and Education:

Laboratory microcosms are good model systems for exploring ecological questions involving long-term population dynamics, such as the questions investigated in this project. Microcosms are particularly suitable for testing ecological theories that are difficult or impossible to test in the field. Findings from our microcosm experiments have prompted us to collaborate with researchers in the school of mathematics at Georgia Tech to develop novel ecological theories. We also have shown microcosm and protist pictures used in this project to undergraduates taking the General Ecology course at Georgia Tech, in an effort to facilitate students' learning and raise their interests in ecological research.

Contributions Beyond Science and Engineering:

Conference Proceedings

Categories for which nothing is reported:

Organizational Partners

Any Web/Internet Site

Any Product

Contributions: To Any Other Disciplines

Contributions: To Any Beyond Science and Engineering

Any Conference